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GLOBAL COMPARISONS OF AQUATIC ECOSYSTEMS*

by

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ABSTRACT

The poster compares the results from analysis of 26 aquatic ecosystems. The ecosystems are ranked after maturity *sensu Odum* and this ranking is compared with a ranking based on system ascendency as proposed by Ulanowicz. From this first and cursory comparison it seems that maturity and ascendency are not correlated.

The transfer efficiencies between consumer trophic levels are compared and it is concluded that the transfer efficiencies mainly fall in the range of 10-20%, the average varying around 15% for all trophic levels.

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INTRODUCTION

Ulanowicz and Wulff (1989) recently presented what they hoped would stand "as a first example [...] of the comparative anatomy of ecosystems" - a detailed comparison between steady-state trophic models of the Baltic Sea and Chesapeake Bay.

The present paper follows on theirs, but differ from it in several features:

(i) we compare 26 systems;

(ii) the systems we compare, however, do not have homologous boxes - nor indeed do they have the same number of boxes;

(iii) because of (ii) we are not comparing the "anatomy" (or better the "physiology") of our systems, but rather we shall try to identify methods and scales by which a taxonomy of ecosystem models could be established.

Such taxonomy would identify classes of systems that may have similar emergent properties, but completely different constituent species.

Identifying (not necessarily linear) scales along which models can be arrayed should help establish such taxonomy, but may also be of immediate interest as such scales would allow for prediction of quantifiable features of ecosystems.

Thus for examples if certain features of models can be shown to be associated with the upper range of a temperature scale (possibly after higher order effects are accounted for), then this may allow prediction pertinent to global climatic changes.

Similarly, a "maturity" scale could be established, based on Odum (1969) who presented 24 properties characterizing ecosystems as they develop (Table 1). These properties can be used for qualitative statements on ecosystem maturity, but so far attempts to make quantitative comparisons between systems had little success.

The work by theoretical ecologist in the SCOR Working Group 59 on "Mathematical Models in Oceanography" (Platt et al. 1981), have however increased our knowledge of the functioning of aquatic ecosystems. To be mentioned especially here is the work summarized in R.E. Ulanowicz (1986) where the concept of "ascendency" is introduced. Ascendency, which has the nonstraightforward dimension of "flowbits" is seen by its inventor as correlating "well with most of Odum's (1969) 24 properties of 'mature' ecosystems" (Ulanowicz and Norden 1990).

This study is an attempt to test this proposition; to do so, we have analyzed 26 aquatic ecosystems using the ECOPATH II model. This includes all of the models we have analyzed to date with ECOPATH II, with the exception of models with less than 10 groups ("boxes") since Pongase (this poster session) has shown that ascendency then becomes largely independent of the number of boxes included in a model.

RESULTS AND DISCUSSION

When ranked according to ascendency the picture shown in Table 2 emerges.

Interpretation of this ranking is not straightforward. A few features make sense, though. Thus the trend for the three Peru models from the 1950s (no fishery) over the 1960s (strong fishery) to the 1970s (fishery collapsed) is as should be expected if unexploited systems mature towards increasing ascendency.

For several of the other systems the ranking is more difficult to understand. E.g., the ascendency of the Lake Victoria ecosystem was higher in the 1980s than in the 1970s even though the introduction of Nile perch (*Lates niloticus*) and overfishing led to an impoverishment of the original highly specious fish fauna.

Thus it appears necessary to include factors other than ascendency in the comparisons. We have done this by also looking at seven of the attributes characterizing ecosystem maturity according to Odum (Table 1). Some of the attributes are used in a transformed form ensuring that a high value should indicate high maturity. The seven attributes (numbered as in Table 1) are,

1) Ratio between primary production and respiration transformed as (-absolute value of ((PP/Resp)-1);

2) Supported biomass, i.e., biomass/ primary production;

3) Biomass/system total throughput;

4) Efficiency of the fishery (total fishery (or harvest)/total primary production);

6) Total biomass of all groups in the system excluding only detritus;

15) Cycling index (%)

16) Proportion of flow supported by the detritus, estimated here as the contribution of flow from detritus to herbivores and detritivores combined.

These seven attributes of maturity (1969) have been extracted from Table 1 as the ones that seems most readily quantifiable. Of importance is also that all the variables that are needed for calculating the attributes are included in the ECOPATH II model already.

As the seven attributes can all be considered measures of maturity, we have used a measure of concordance to investigate the degree of coherence. Using Kendall's coefficient of concordance (Siegel and Castellan 1988) we find that there is a high (S.L. < 0.001) degree of concordance and we conclude that the rankings based on the seven measures can be expressed on a common scale - they can all be ranked after maturity *sensu Odum*. The resulting ranking is given in Table 3, together with the ranking based on ascendency. We have compared these two rankings using Kendall's rank-order correlation (with tied observations) and had to accept the null hypothesis that the two rankings are independent. We do thus not find that the ascendency is related to maturity.

We find it necessary though to call for caution; as the present comparisons are done in a very rough manner without standardizing the ecosystem descriptions. Most important here is perhaps the remineralization conducted by bacteria. For most groups this dominant flow is neglected. The most sensible approach is probably to disregard the bacteria remineralization bearing in mind the present controversy on methods for estimating bacterial production (see recent discussion, in Aquabyte). This may solve part of the problem, but not all, as e.g., it will not explain why the model for the Peru upwelling system in the 1950's has lower rank than the models for the two following decades, nor will it explain why the Lake Victoria model for 1985 is ranked higher than the model for 1971.

We must conclude that the present attempt to compare ecosystems is only of a preliminary nature. A more refined approach examining the maturity concept in more detail and including more ecosystems is needed.

TROPHIC EFFICIENCIES

As described by Christensen and Pauly ("ECOPATH II Model", this session) it is possible to distribute the groups in a system on discrete trophic levels *sensu* Lindeman. We have done this for 12 ecosystems, and expressed the findings using the pyramids on Fig. 1. The volume of the pyramids are all scaled according to system throughput, and are all expressed in gram wet weight/m^2/year. Conversion of throughput expressed in other units have been done using the same conversion factors as Steele (1974), i.e. 1 g wet weight = 1 kcal and 1 g carbon in organic matter = 10 kcal = 10 g wet weight.

The pyramids can be compared. The first question which arise probably is: why are the sizes so different? Truly, they are different, but they were also put on the same scale without logarithmic transformation.

It should be noted here that the systems have not been thoroughly standardized. Thus it will for instance be of major importance if the previously mentioned detritus-bacteria flow responsible for remineralization is included or not. The standardization when completed will change some of the pyramids, but it will not affect the major finding: throughput varies and the pyramids show it.

The pyramids show more. The "steps sizes" on the pyramids show the throughput at each trophic level. Comparisons of consecutive steps thus give an idea of transfer efficiencies. These can be calculated and compared as on Fig. 2 where conversion efficiency is plotted against discrete trophic levels (consumers only). Each line on the figure represents an ecosystem (same as in Table 1).

As can be seen from the figure, the efficiencies varies but there is a consistent tendency that the efficiencies are in the range between 10 and 20 per cent. For most cases, the efficiencies only varies slightly between trophic levels within a system.

The average efficiencies do not show any trend over the observed range of trophic levels. Thus on the average 15% of the flow entering a trophic level is passed on to the next trophic level.

CONCLUDING REMARK

A global picture is necessary for a global comparison. Up to now we did not have the data needed for a thorough analysis, and we have seen the problem arising from not standardized investigations presented in a non-standardized manner. We have faith however that this poster session will bring us a big step forward, and that analysis including all the data sets we see here will cast new light on the globe.

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Table 1. A tabular model of ecological succession: trends to be expected in the development of ecosystems.*

	Ecosystem attributes	*Developmental states*	*Mature stages*
		Community energetics	
1	Gross production/community respiration (P/R ratio)	Greater or less	Approaches 1
2	Gross production/standing crop/ biomass (P/B ratio)	High	Low
3	Biomass supported/unit energy flow (B/E ratio)	Low	High
4	Net community production (yield)	High	Low
5	Food chains	Linear, predominantly grazing	Weblike, predominantly detritus
		Community structure	
6	Total organic matter	Small	Large
7	Inorganic nutrients	Extrabiotic	Intrabiotic
8	Species diversity-variety component	Low	High
9	Species diversity-equitability component	Low	High
10	Biochemical diversity	Low	High
11	Stratification and spatial heterogeneity (pattern diversity)	Poorly organized	Well-organized
		Life history	
12	Niche specialization	Broad	Narrow
13	Size of organism	Small	Large
14	Life cycles	Short, simple	Long, complex
		Nutrient cycling	
15	Mineral cycles	Open	Closed
16	Nutrient exchange rate, between organisms and environment	Rapid	Slow
17	Role of detritus in nutrient regeneration	Unimportant	Important
		Selection pressure	
18	Growth form	For rapid growth ("*r*-selection")	For feedback control ("*K*-selection)
19	Production	Quantity	Quantity
		Overall homeostasis	
20	Internal symbiosis	Undeveloped	Developed
21	Nutrient conservation	Poor	Good
22	Stability (resistance to external perturbations)	Poor	Good
23	Entropy	High	Low
24	Information	Low	High

* Odum, E.P. 1969. The strategy of ecosystem development. Science 104:262-270.

Table 2. Ranking of 26 ecosystems after ascendency as proposed by Ulanowicz. In addition, 7 measures of maturity *sensu Odum* are given. These measures are numbered in the bottom line with the same numbers as used in Table 1.

System	Ref.	Asc. %	Total biomass	Cycling %	PP/ Resp.	-ABS (P/R-1)	Biom. /PP	Flow from det.(%)	Biom./ Tr.put	Fish. eff.
Crystal River, Florida	1	40.1	12.2	4.6	0.79	-0.21	0.25	98	0.05	
G.o.Mexico, Sheridan	2	39.0	76.8	5.2	0.45	-0.55	0.03	39	0.00	0.0036
Hatteras	3	36.0	11.0	1.9	0.25	-0.75	0.04	38	0.01	0.0021
French Frigate, Hawaii	4	34.8	174.6	7.2	4.27	-3.27	0.05		0.08	
Chesapeake Bay	5	34.7	109.6	18.7	0.34	-0.66	0.03	91	0.00	0.0166
ChinaPolyculture	6	34.4	1,289.8	1.4	2.07	-1.07	0.06	29	0.01	0.0192
Rybinsk Reservoir	7	32.2	12.0	16.6	0.36	-0.64	0.02	96	0.00	0.0016
G.o.Mexico, Browder	8	27.7	34.9	8.4	1.00	-0.00	0.04	29	0.01	0.0029
Campeche Bank, Mexico	9	27.0	684.7	17.3	0.98	-0.02	0.17	58	0.04	0.0012
Yucatan Shelf, Mexico	10	26.9	385.8	21.6	1.00	0.00	0.11	65	0.03	0.0000
Western G.o.Mexico	11	26.6	66.2	19.0	1.00	-0.00	0.13	57	0.03	0.0013
Schlei Fjord, Kiel	12	25.4	201.9	21.6	1.00	-0.00	0.26	41	0.07	0.0037
Peru Upw. 1950	13	25.0	377.9	3.7	1.44	-0.44	0.03	6	0.01	0.0006
Tamiahua Lagoon, Mexico	14	25.0	8.4	11.8	1.00	0.00	0.11	51	0.04	
Peru Upw. 1960	15	23.2	406.2	5.0	1.01	-0.01	0.03	10	0.01	0.0093
Peru Upw. 1970	16	22.7	403.9	7.3	1.00	-0.00	0.03	10	0.01	0.0034
Lake Victoria 1985	17	22.3	105.9	3.9	1.46	-0.46	0.05	10	0.02	0.0082
Lake Aydat, France	18	22.1	309.4	14.6	1.00	-0.00	0.09	41	0.03	
Lake Victoria 1971	19	21.9	84.6	3.4	1.65	-0.65	0.04	10	0.02	0.0016
Sierra Leone Estuary	20	21.9	34.8	3.0	1.01	-0.01	0.02	26	0.01	0.0105
Terengganu Coast., Malaysia	21	21.4	52.6	20.4	1.01	-0.01	0.03	45	0.01	0.0056
Bukit Reservoir, Malaysia	22	20.3	25.9	9.2	0.64	-0.36	0.26	36	0.06	0.0418
Cornwall Mud Flat	23	20.0	182.2	4.1	0.36	-0.64	0.11	23	0.04	
Sierra Leone Mudbottom	24	17.1	29.0	5.4	1.01	-0.01	0.02	32	0.01	0.0122
Brunei Coatal Area	25	15.9	21.6	11.3	1.68	-0.68	0.02	49	0.01	0.0008
Celestun Lagoon, Mexico	26	15.0	552.7	28.5	0.61	-0.39	0.29	71	0.04	0.0000
Odum Maturity No.			6	15		1	2	17	3	4

Sources: (1) Ulanowicz (1986); (2) Sheridan et al. (1984); (3) Walsh (1988); (4) Polovina (1984); (5) Baird & Ulanowicz (1989); (6) Ruddle & Christensen (this vol.); (7) Yu Sorokin (1979); (8) Browder (this vol.); (9) Vega-Cendejas et al. (this vol.); (10) Arreguin-Sanchez et al. (a, this vol.); (11) Arreguin-Sanchez et al. (b, this vol.) (12) Nauen (1984); (13) Jarre et al. (in press); (14) Abarca-Arenas & Valero-Pacheco (this vol.); (15) as in 13; (16) as in 13; (17) Moreau et al. (this vol.); (18) Reyes-Marchant et al. (this vol.); (19) as in 17; (20) Longhurst (1983); (21) Liew & Chan (1987); (22) Yap (1983); (23) Warwick et al. (1978); (24) as in 20; (25) G. Silvestre et al. (this vol.); (26) Chavez et al. (this vol.)

Table 3. Ranking of 26 ecosystems after ascendency and after maturity sensu Odum. Lowest number indicates highest rank (value, references to sources are given in Table 2.

Ascendency		Maturity	
1	Crystal River, Florida	1	Schlei Fjord, Kiel
2	G.o.Mexico, Sheridan	2	Celestun Lagoon, Mexico
3	Hatteras	3	Yucatan Shelf, Mexico
4	French Frigate, Hawaii	4	Campeche Bank, Mexico
5	Chesapeake Bay	5	Western G.o.Mexico
6	China Polyculture	6	Bukit Reservoir, Malaysia
7	Rybinsk Reservoir	7	Lake Aydat, France
8	G.o.Mexico, Browder	8	Terengganu Coastal, Malaysia
9	Campeche Bank, Mexico	9	Tamiahua Lagoon, Mexico
10	Yucatan Shelf, Mexico	10	Crystal River, Florida
11	Western G.o.Mexico	11	Chesapeake Bay
12	Schlei Fjord, Kiel	12	Peru Upw. 1960
13	Peru Upw. 1950	13	Peru Upw. 1970
14	Tamiahua Lagoon, Mexico	14	G.o.Mexico, Browder
15	Peru Upw. 1960	15	China Polycutlure
16	Peru Upw. 1970	16	Lake Victoria 1985
17	Lake Victoria 1985	17	Cornwall Mud Flat
18	Lake Aydat, France	18	Sierra Leone Mudbottom
19	Lake Victoria 1971	19	French Frigate, Hawaii
20	Sierra Leone estuary	20	Rybinsk Reservoir
21	Terengganu Coastal, Malaysia	20	G.o.Mexico, Sheridan
22	Bukit Reservoir, Malaysia	22	Lake Victoria 1971
23	Cornwall Mud Flat	23	Sierra Leone Estuary
24	Sierra Leone Mudbottom	24	Peru Upw. 1950
25	Brunei Coastal Area	25	Brunei Coastal Area
26	Celestun Lagoon, Mexico	26	Hatteras

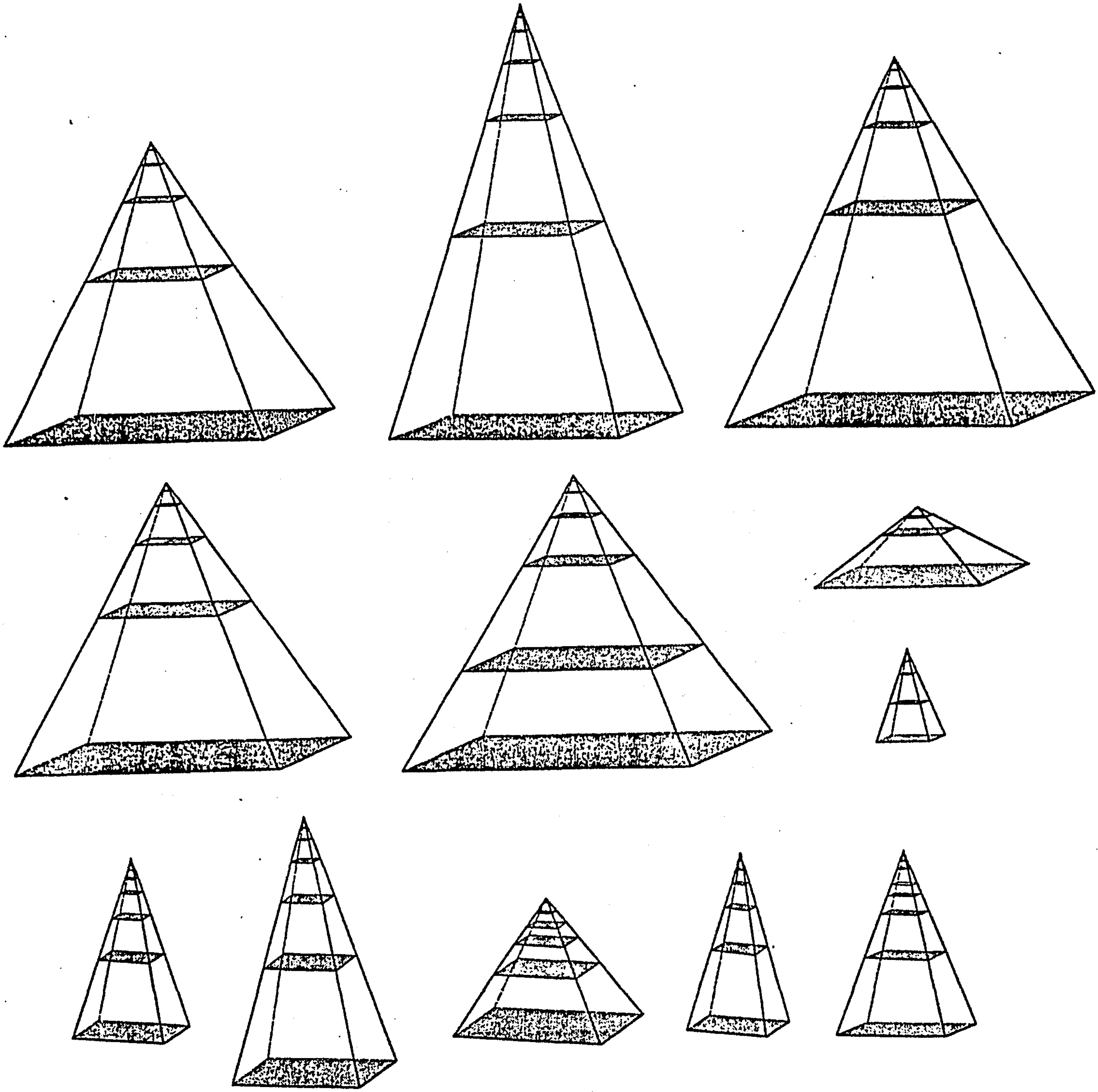

Fig. 1. Lindeman pyramids for 12 ecosystems. All pyramids are shown on the same relative scale, and are thus comparable. The pyramid volumes are proportional to the total system throughputs. The ecosystems are:

(1)	Peru upwelling 1960s	(7)	Bukit Merah reservoir, Malaysia
(2)	Peru upwelling 1970s	(8)	Mudbottom, Sierra Leone
(3)	China polyculture pond	(9)	Terengganu, Malaysia
(4)	Peru upwelling 1950s	(10)	Rybinsk reservoir, USSR
(5)	Chesapeake Bay, USA	(11)	Estuary, Sierra Leone
(6)	Schlei Fjord, Germany	(12)	French Frigate Shoals

For references see Table 2.

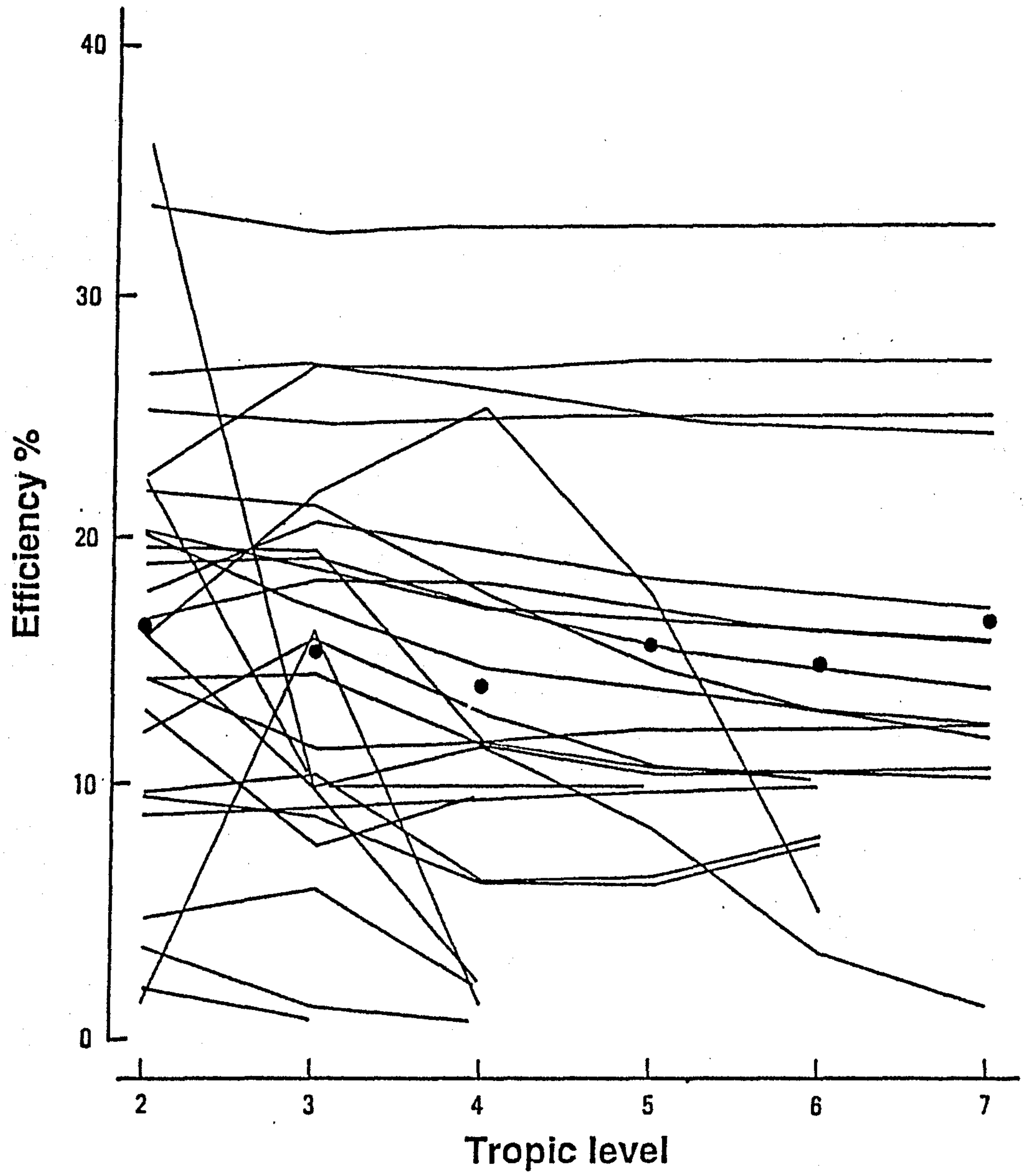

Fig. 2. Conversion efficiency (%) by discrete trophic level *sensu* Lindeman for 26 ecosystems. The dots on the figure indicates the average efficiencies by trophic level. Efficiency seems to decrease with 1.5% for each trophic level up the Lindeman pyramid.